Stem radial growth and water storage responses to heat and drought vary between conifers with differing hydraulic strategies

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Abstract

We investigated stem radial growth and water storage dynamics of two conifer species differing in hydraulic-carbon strategies, *Juniperus monosperma* and *Pinus edulis*, under conditions of ambient, drought (~45% reduction in precipitation), heat (~4.8 ºC temperature increase) and the combination of drought+heat, in 2013 and 2014. Juniper maintained low growth across all treatments. Overall, the relatively isohydric piñon pine showed significantly greater growth and water storage recharge than the relatively anisohydric juniper across all treatments in the average climate year (2014) but no differences in the regionally dry year (2013). Piñon pine ceased growth at a constant pre-dawn water potential across all treatments and at a less negative water potential threshold than juniper. Heat has a greater negative impact on piñon pines' growth and water storage than drought, while juniper was, in contrast, unaffected by heat but strongly impacted by drought.The whole-plant hydraulic-carbon strategies, in this case captured using the iso/anisohydry concept, translate into alternative growth and water storage strategies under drought and heat conditions.

Key words: Increased temperature; LVDT; *Juniperus monosperma*; growth; *Pinus edulis;* water potential.

Brief summary

The study included heat treatments within a drought study in a multi-factorial manner on mature trees, and investigated stem radial growth and water storage dynamics of two conifer species differing in hydraulic-carbon strategies. We found that the relatively isohydric piñon pine was more sensitive to heat and drought than the relatively anisohydric juniper. Our results further suggest that heat has a greater negative impact on piñon pine growth and water storage than drought.

Introduction

Among the potential effects of warming climate across terrestrial biomes are impacts on growth and survival of trees. Significant forest mortality events have been documented for many regions in all major forest biomes in relation to warming and drought (Allen et al. 2015**)**. Trees that experience growth reductions from drought and temperature stress are often more prone to drought-induced mortality (Waring 1987; Bigler et al. 2006; McDowell et al. 2010; Kane and Kolb 2010; Macalady and Bugmann 2014; Cailleret et al. 2017). Heat may exacerbate the impacts of drought (Adams et al. 2009; 2015; 2017; Williams et al. 2013; Allen et al. 2015), and growth and development are highly sensitive to stress from water availability (Korner 2003; Fatichi et al. 2014). Radial growth is also affected by dynamics of water storage that can modify the water potential of xylem and cell turgor during the enlargement phase (Taiz and Zeiger 1998; Turcotte et al. 2011).

Water stored in plant tissues has long been recognized as an important factor in transient regulation of plant water relations (Meinzer et al. 2004). There is evidence that water storage in plants is an adaptation that helps plants overcome drought (Holbrook 1995). The avoidance of embolism is achieved in part via transient release of stored water to constrain fluctuations in xylem tension, so the buffering influence of water storage can be viewed as a dynamic component of overall hydraulic safety (Meinzer et al. 2009). The dependence of trees on stored water on diel time scales increases with drought (Phillips et al. 2003), but the impact of heat is poorly understood.

Heat can impact stem radial growth and water recharge via direct and indirect mechanisms. Radial growth depends on carbohydrate availability and on suitable cell water potential for growth, both of which may be limited under conditions of elevated temperature due to the impact of temperature on vapor pressure deficit, with both potentially pushing trees to reduce photosynthesis (and hence growth) via sub-optimal temperature for photosynthesis,

via heat damage to photosynthetic proteins, or simply via prolonged stomatal closure (McDowell et al. 2008; Turcotte et al. 2011). Warmer temperatures impact vapor pressure deficit (Trenberth et al. 2014), which may increase water recharge rates when soil water is available; though if heating results in lower soil water availability then rising VPD forces greater risk of mortality (e.g. McDowell and Allen 2015). Drought-mortality studies consistently show that warmer temperatures kill trees faster (reviewed by Allen et al. 2015; also see Adams et al. 2017), and studies suggest heat negatively impacts stem radial growth in conifers (Pichler and Oberhuber 2007; Williams et al. 2013; Ruehr et al. 2015).

Continuous stem diameter measurements offer excellent quality and resolution for evaluating growth (Zweifel et al. 2010; Mencuccini et al. 2013; Mencuccini et al. 2017) and tree water relations in response to environmental factors (see e.g. Irvine and Grace 1997; Sevanto et al. 2001; Sevanto et al. 2005a). These measurements allow for quantifying both growth (irreversible swelling) and changes in water storage (reversible swelling) at high temporal resolution.

In this study, we examined growth and water storage responses to drought and heat within the iso/anisohydric framework of water potential variation. Iso/anisohydric classification schemes have been used to label different responses in stomatal closure at different vapor pressure deficits or leaf water potentials during drought (see e.g. Hochberg et al. 2018) but extends to impacts on carbon metabolism and xylem embolism via relationships of these processes with stomatal closure (e.g. McDowell et al. 2008; Klein 2014; Martínez-Vilalta et al. 2014; Skelton et al. 2015). In southwestern USA the relatively isohydric species piñon pine (*Pinus edulis*) closes stomata more rapidly during drought than the relatively anisohydric juniper (*Juniperus monsperma*; McDowell et al. 2008), leading to lower photosynthesis (Limousin et al. 2013) and carbohydrate storage (Dickman et al. 2015) during drought. Due to differences in xylem vulnerability, the isohydric species in this system is

more prone to xylem embolism than the anisohydric species, despite the isohydric species maintaining higher water potentials (Garcia-Forner et al. 2016). The link between stomatal regulation during drought and associated impacts on growth and water storage among tree species remains an open question with important implications for our ability to understand and model plant drought responses (McDowell et al. 2013; Martínez-Vilalta and Garcia-Forner 2016).

We used a unique ecosystem-scale field manipulation of air temperature and drought on two semi-arid conifer species, piñon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*) in northern New Mexico, USA, to test the hypothesis that iso/anisohydric patterns in stomatal closure during drought translate into differential growth and water storage behavior under drought and heat conditions. Specifically, we hypothesized that anisohydric (greater stomatal conductance during drought) behavior would allow juniper to grow more than pine, particularly under conditions of drought and/or heat. Given the lower xylem embolism of juniper than pine at this site (Garcia-Forner et al. 2016), we hypothesized that pine would require greater stem water recharge to compensate for losses during drought and/or heat stress. Based on the observations that heat negatively impacts conifers in this region (Williams et al. 2013), we further hypothesized that heat would impair pine more than juniper given its more sensitive stomatal responses to environmental conditions.

Materials and Methods

Site description and experimental design

The Los Alamos Survival-Mortality experiment (SUMO) is located near Los Alamos, New Mexico, USA. The experiment is located in a piñon-juniper woodland near the ponderosa pine (*Pinus ponderosa*) forest ecotone at 35°49’5” N, 106°18’19” W (Adams et al., 2015), at an elevation of 2150 m (Garcia-Forner et al. 2016). Mean annual temperature

from 1987-2013 was 10.5°C with the coldest month (January) averaging -2 °C and warmest month (July) averaging 20°C. Mean annual precipitation is 414 mm of which ~48% falls during the North American Monsoon between July and September. Mean annual temperature in 2013 was 9.7°C and total precipitation was 426 mm. Mean annual temperature in 2014 was 10.9°C and total precipitation was 330 mm (http://environweb.lanl.gov/weathermachine/). The woodland is dominated by piñon pine (*Pinus edulis Engelm.*) and one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg.); gambel oak (*Quercus gambelii* Nutt.) and ponderosa pine (*Pinus ponderosa* C. Lawson) occur in the vicinity (Garcia-Forner et al., 2016). Soils are Hackroy clay loam and range in depth from 40 to 80 cm above a parent material of volcanic tuff (Adams et al., 2015).

The SUMO experiment includes a below canopy rain-out structure that diverts ~45% of precipitation off the site, and transparent, open-top chambers (OTCs) regulated by heating and cooling units (RJPL Package Heat Pump and RLPL Package Air Conditioner, Rheem Manufacturing Company, Atlanta, GA, USA) to enable temperature control (Garcia-Forner et al. 2016). In total 24 trees were selected for the experiment, 12 piñon pine and 12 one-seed juniper trees characterized by an average diameter of 16.4 ±3.2 cm and 17.3±5.2 cm respectively and leaf area estimates of 29.7±3.7 m^2 for pine and 30.5±8.3 m^2 for juniper trees (McBranch et al *in revision*). The selected trees were assigned to four treatments: ambient (ambient precipitation and temperature), drought (~45% rain-out), heat (~+4.8°C OTC), and drought+heat (~45% rain-out and ~+4.8°C OTC).

Temperature was monitored by two weather stations at the site and in each OTC at two heights (1 m and 2/3 tree height; CS215 Temperature and Relative Humidity Probe and CR1000 datalogger, Campbell Scientific, Logan, UT, USA). This system was used as a thermostat to set desired temperature conditions in chamber (Adams et al., 2015). The

treatments were initiated in early June 2012 (Garcia-Forner et al. 2016). The mean temperature increase in the heated treatment (heat and drought+heat) was +4.77°C, mean vapor pressure deficit differences from ambient site conditions were +0.36 kPa for heat, +0.01 kPa for drought, and +0.69 kPa for drought+heat treatments (Adams et al., 2015).

Stem radial growth and water storage measurements

We used measurements of changes in tree stem diameter to determine stem radial growth and water storage recharge after precipitation events. Growth activity can be discontinuous in space, with greater increments at top of stem than at the base. Sometimes, trees that complete xylem increments in the upper stem do not grow at all in the lower stem (Kozlowsky and Pallardy 1997). At our site, such differences could be enhanced because of the very water-limited environment, as well as manipulations by the drought and heat treatments (Adams et al. 2015). Thus, we measured both upper and lower stem diameter changes. Diameter variations were measured with linear variable displacement transducers (LVDT; Solartron AX/5.0/S, Solartron Inc., West Sussex, UK) attached to a rectangular metal frame mounted around the stem (see e.g. Sevanto et al. 2011). Two sensors were placed on each tree: one at the base below the canopy (0.1-0.5m height) and one at the top at approximately 2/3 of the total tree height, which varied between 1.5 and 4.5m. The sensors were secured to a metal frame attached to the stem with screws. The sensor tip was set on smoothed bark where most of the dead bark was removed, leaving a thin layer to protect the phloem from evaporative water loss (Sevanto et al. 2005b). Measurements were conducted every minute on two trees of each species in drought, drought+heat and ambient treatments in 2013 and three trees of each species in drought, heat, drought+heat and ambient treatments in 2014.

Diameter variation calculations

The diameter sensor measurement data indicate a relative change in diameter over time. To analyze the data for growth in each summer we set the value at zero on the first midnight of the measurement period (1 May) when no growth was yet occurring (McDowell et al. 2010; Adams et al. 2015). The selection of the reference state, taken here as the first midnight of the time series, is for practical convenience and has only a minor effect on the calculated values of the biophysical parameters (Mencuccini et al. 2013).

In this study, the timing of growth initiation (phenology) was defined for each tree and each sensor by the day on which daily maximum stem diameter (typically at midnight) exceeded the culmination point of the daily maximum diameter of the stem on the previous day (Zweifel et al., 2010). The end of the growth period was defined as the first day for which the daily maximum diameter of the stem after a rainfall event (when the swelling and shrinking process had finished) began a decreasing trend. Growth occurred both during and outside rainfall events, and swelling of tree trunks resulting from replenishment of stem water stores was excluded from the growth estimates.

Tree water storage recharge after rainfall events

To determine the recharge of stem water reserves after a rainfall event, we first removed growth from the diameter variation data, because the elastic (non-growth) response to precipitation events is our focus herein. This was done by subtracting a linear growth function from the data of the growth period defined as explained above. The volume of storage water (ΔV) obtained during each precipitation event was calculated as the difference between the initial volume of a stem segment around the diameter variation sensors before a

rainfall event (V) and the new volume of the stem segment after a rainfall event (V') (Génard et al. (2001)

$$\Delta V = V' - V = \pi l \frac{(D+\Delta D)^2}{4} - \pi l \frac{D^2}{4} = \frac{\pi l}{4}(2D\Delta D + \Delta D^2) \quad (1)$$

where D is the stem diameter at the measurement site, ΔD is the observed change in diameter, and l the length of the segment considered. Since ΔD is typically of the order of magnitude 0.1 mm, while D is of the order of magnitude 10 mm (Sevanto et al. 2002), ΔV can be approximated by

$$\Delta V \cong \frac{\pi l}{2}(D\Delta D) \quad (2)$$

Eq. 2 gives the volume change of segments of length l for each precipitation event. We used the representative segment length of 1 mm to evaluate local water storage at each sensor location. This approach was chosen to eliminate any influence of stem tapering and deviations from cylindrical form that could affect the estimates if using segments much longer than the measurement represents. Finally, to consider the differences in tree size, ΔV of eq. 2 was divided by the mean diameter of each tree at breast height for piñon pine while for juniper it was divided by the mean diameter at breast height of all stems of each tree. In this manner, we analyzed every precipitation event between May to September of 2013 and 2014 to compare the influence of species and treatment on the recharge capacity of trees.

Pre-dawn Leaf Water potential

Leaf water potential of each tree was measured once per month to determine how its variation affected growth. For each measurement, two twig samples were excised from the south side of each tree before sunrise (predawn water potential, Ψ_{pd}) and kept in the dark in a refrigerator at the site until measurement within two hours of collection. Water potential was measured with a Scholander-type pressure chamber (PMS Instruments, Albany, OR, USA)

and determined as the mean of the two samples for each tree. Pre-dawn leaf water potential data were fitted with a sigmoid regression curve (Weibull) vs growth and leaf water potential corresponding to zero growth was estimated as the inflection point (defined as the transition from the initial curvilinear, steeper part of the curve, to the more linear and less steep part).

Data analysis

Prior to data analysis, diameter variation time series for each sensor and tree were quality-checked and outliers resulting from movement of the frame or electrical noise were corrected or removed. To test for species and treatment differences in tree growth rate, at each sensor position (base and top), a linear mixed model was developed to describe differences in daily maximum stem diameter between species. The model considered the following as fixed factors: treatments (ambient, drought, heat, and drought+heat), species and the interactions between treatments and species. Individual trees were input as a random effect. An AR (1) autoregressive correlation structure was included to allow for lack-of-independence over time among measurements for each day. Post-hoc analysis was performed with Tukey's HSD test for multiple comparison. For all analyses, we defined statistical significance as $\alpha = 0.05$. Analyses of linear mixed models were performed using R software (v. 3.0.1, R Foundation for Statistical Computing) using the nlme package. The remaining statistical analyses were performed in SPSS Statistics 20.0 (SPSS Inc., Chicago, IL, USA). For analysis of phenology (timing of growth initiation), a general linear model analysis of covariance (ANCOVA) was constructed using treatments and species as factors (Tukey's HSD post-hoc test). To determine the leaf water potential at which growth ceases we fitted a Weibull curve to the growth vs. leaf water potential data. Leaf water potential was measured only once a month, while growth was measured continuously. To match the data sets, we considered the cumulative growth obtained between each measurement interval of leaf water potential as a representative of growth. The leaf water potential at which growth ceases was

determined from the inflection points of the Weibull curves. Confidence intervals of the model (95%) and its inflection points were calculated to test differences between treatments. For the analysis of stem volume storage dynamics and rainfall pulses, we calculated treatment means for top and base sensor separately and used linear regression. Finally, a general linear model ANCOVA was used to test the homogeneity of regression slopes for the relationships between rainfall pulses and stem volume storage dynamics between species and treatments (for the drought treatment, measured rainfall was reduced by 45% according to the calculated treatment effect).

Results

Growth and phenology

Stem growth was low for both species, and not significantly different from each other, in 2013 (<0.17 mm average for piñon pine; <0.13 mm average for juniper) (Figure 1). The lack of growth in 2013 corresponded to a regional drought. From January through August 2013, the SUMO experiment site received only 146 mm of precipitation, 51% of the 25-year mean of 284 mm for the same period (Adams et al., 2015, Grossiord et al., 2017). The annual precipitation neared the long-term average only after a very large rainfall event in September (Adams et al. 2015). From May to September 2014 our hypothesis that juniper would grow more than pine was not supported. In both base and top sensors, stem radial growth was higher in piñon pine than juniper (Table S1, Figure 2). In the top sensors, differences between the two species were greatest for ambient and drought treatments (Table S1, Figure 2). In the base sensors, stem radial growth was greater for piñon pine than juniper for the ambient treatment (Table S1, Figure 2). Due to the larger treatment effects and greater sample size during the wetter 2014, we focus the remainder of our results on data from 2014.

Heat had the greatest impact on stem radial growth in pine while drought had a larger impact on juniper. Within piñon pine, stem radial growth was higher in ambient and drought than for the two heated treatments (for both base and top sensors, Figure 2). In contrast, for juniper top sensors, stem radial growth was greatest for ambient and both heat treatments (i.e. heat and drought+heat treatments; Figure 2) while drought significantly reduced juniper stem radial growth. In juniper base sensors, stem radial growth was greatest for ambient and heat treatments, while drought treatments (i.e. heat and drought+heat treatments) significantly reduced growth.

Mean growth initiation in piñon pine top sensors occurred at approximately the same time in ambient, drought and heat treatments, while growth initiation in drought+heat treatment was delayed 67 days relative to ambient ($p < 0.05$, ANCOVA analysis and post-hoc Dunn's test, Figure 3). There were no significant treatment differences in the mean timing of growth initiation of piñon pine base sensors. Mean juniper growth initiation exhibited no significant treatment differences in the mean timing of growth initiation at either sensor height ($p > 0.05$, ANCOVA, Figure 3). Mean piñon pine growth initiation for all treatments was day of year 147±9 and for juniper for all treatments was day of year 160±12, but these differences were not significant ($p > 0.05$, ANCOVA).

Predawn leaf water potential of stem radial growth cessation

To compare growth responses within one of the iso/anisohydric frameworks, we examined the pre-dawn leaf water potential associated with cessation of growth, similar to estimates of the pre-dawn water potential associated with zero stomatal conductance or photosynthesis (e.g. McDowell et al. 2008; Skelton et al. 2015; Hochberg et al. 2018). The average Ψ_{pd} of zero growth in 2013 and 2014 did not differ between treatments for either species. The 95% confidence intervals of Weibull fits overlapped within treatments for both top and base sensors within species (see Figure 4, Supporting Information Figure S2, S3). For

the base sensors, there were significant differences between species in the Ψ_{pd} of zero growth depending on the treatment (Figure 4). Significant differences were found only in the drought treatment. No significant differences were found for the other treatments.

Consistent with their differing iso/anisohydric characteristics and drought tolerances, piñon pine's Ψ_{pd} of zero growth under drought was -1.31 MPa (95% confidence interval, -0.81 to -1.81 MPa), whereas for juniper it was -2.06MPa (95% confidence interval, -1.86 to -2.06 MPa). These results indicate that juniper continues to grow at lower water potential than piñon pine under drought, consistent with the much more negative water potentials juniper experiences than pine in this system (McDowell et al. 2008, Breshears et al. 2009; Grossiord et al. 2017).

Reversible volume response to precipitation

Volume storage (elastic water storage, non-growth) of juniper and piñon were positively and significantly correlated with rainfall pulses ($p < 0.05$, Figure 5), with higher rain pulses resulting in larger recharge both at the base and the top. Significant differences in the relationship between stem volume storage and rainfall pulse amount between species and treatments were observed ($p < 0.001$, ANCOVA). Consistent to our iso/anisohydry based predictions, piñon stored significantly more water for a given amount of precipitation than juniper, for all treatments in top sensors and for drought+heat treatment in base sensors ($p < 0.001$). Similar to the stem radial growth results previously shown, piñon top stems stored significantly less water for a given amount of precipitation in heat and drought+heat treatments than drought and ambient treatments, with reduced water storage for both heat treatments ($p < 0.001$, ANCOVA, Figure5). Juniper bottom stems stored significantly more water for a given amount of precipitation in drought and drought+heat treatments than in ambient and heat treatments, with increased water storage under both drought treatments ($p < 0.001$, ANCOVA, Figure 5).

Discussion

Piñon pine and juniper exhibited strongly divergent responses to drought and increased temperature in this study. Our initial hypothesis was that juniper would exhibit greater growth than pine, particularly under drought or heat, due to its greater stomatal conductance that should allow faster and larger responses to rainfall via greater growth potential both from source (photosynthesis) and sink (embolism impacts on water availability for cell division) limitations. Likewise, due to its lower embolism under drought, we predicted juniper would require less stem water recharge than pine, which experiences significant embolism (Garcia-Forner et al. 2016). The first hypotheses failed as juniper appeared to exhibit a conservative growth strategy compared to pine. The second hypothesis was supported, as juniper had much lower stem water recharge than pine. Beyond these tests, most of the species comparisons exhibited significant differences that may be related to their respective locations on the iso/anisohydric continuum.

Consistent with our final hypothesis, piñon pine was far more affected by heat treatments than juniper (Figures 2-5). However, juniper was significantly impacted by drought (Figures 2-5). Juniper showed low growth but maintained it at relatively negative water potentials, whereas pine exhibited considerably greater growth but was impacted by warm conditions and ceased growing at relatively less negative pre-dawn leaf water potential values (Figure 4). This is consistent with how these two species differ in photosynthesis, with piñon pine ceasing photosynthesis at relatively less negative water potential while juniper maintains photosynthesis during relatively more negative water potential (West et al. 2007, Breshears et al. 2009, Plaut et al. 2012, Garcia-Forner et al. 2016). These species differences

in the pre-dawn leaf water potential at which growth ceased were particularly noticeable in the base sensors, suggesting that this part of the stem is more closely connected to soil conditions than the top (Waring 1978). There were no differences in the Ψ_{pd} of cessation of growth across treatments (Figure 3), thus, no detectable acclimation of stem radial growth to water stress occurred for either species.

Piñon pine exhibited significantly greater growth than juniper (Figure 2), suggesting that it prioritizes growing, even under dry or hot conditions, whereas juniper is more conservative. The low juniper stem radial growth (Figure 2) is consistent with prior observations of juniper's low shoot growth rates (Howell 1941, Herman 1956; Adams et al., 2015). This conservative growth may facilitate juniper's dominance of warmer and more drought-prone locations than piñon pine (Padien and Lajtha 1992) and its widespread survival of a severe regional drought in 2002–2003 that killed vast areas of piñon pine (Breshears et al. 2005). The delay in radial growth initiation under the drought+heat treatment in pine was consistent with foliar phenology results from this site for 2013, in which either a ~2-month delay in needle emergence in main-axis branches or a complete lack of needle growth in side branches on piñon pine was observed in the drought+heat treatment (Adams et al. 2015).

Water uptake to stem stores after rain pulses was greater for piñon pine than juniper (Figure 5), in agreement with our last hypothesis. Water storage capacity varies considerably among plant species and growth forms (Waring and Running 1978, Hunt et al. 1991, Goldstein et al. 1998). Similar to the growth responses (Figures 3, 4), piñon pine water uptake was negatively impacted by both heat treatments whereas juniper was more impacted by drought. In pine, trees in the heat and drought+heat treatments had reduced water storage in upper canopy stems following rainfall relative to ambient treatment trees. In contrast, juniper saw increased water storage at the base of the tree following rainfall under drought treatment relative to ambient. These results are consistent with prior observations that pine

responds rapidly to rain pulses whereas juniper has dampened responses after drought (West et al. 2008), possibly due to the pine's ability to rapidly refill embolized roots (West et al. 2007), as well as with observations of pine shifting its water uptake to deeper soil layers under drought (Grossiord et al. 2017). In a previous drought study on these two species, plant water status was not correlated with pulse responses of transpiration, but reduced leaf area and reduced hydraulic conductance (due to higher antecedent embolism) were speculated to drive lower rainfall pulse responses (Plaut et al. 2013). According to Scholz et al. (2011), above a minimum threshold value of capacitance, trees survive by using capacitance to provide hydraulic safety by buffering fluctuations in tension. The greater water storage of pine than juniper may confer some advantage under future conditions, however, pine's significant reductions in water storage due to warming may predispose it to greater hydraulic risks under future warming temperatures.

The lack of differences in 2013 compared to 2014 was primarily driven by regional hydroclimate, with a severe drought in 2013 resulting in minimal differences in many properties of the system such as soil water content, leaf water potentials, and gas exchange (Garcia-Forner et al. 2016; Grossiord et al. 2017). Under these conditions, little treatment or species differences could be detected, in comparison to the wetter 2014 conditions that allowed larger treatment impacts.

Our study uniquely included heat treatments within a drought study in a multi-factorial manner on mature trees, and investigated stem radial growth and water recharge in two species at opposite ends of the spectrum on their hydraulic-carbon strategies. We found that the relatively isohydric piñon pine was more sensitive to heat and drought than the relatively anisohydric juniper. Our results further suggest that heat has a greater negative impact on piñon pine growth and water storage than drought. This is concerning in light of the chronic temperature increase that is projected both in Southwest USA and globally (Allen

et al. 2015) and is consistent with predictions of widespread pine mortality in the region under future climate scenarios (Williams et al. 2013, McDowell et al. 2016).

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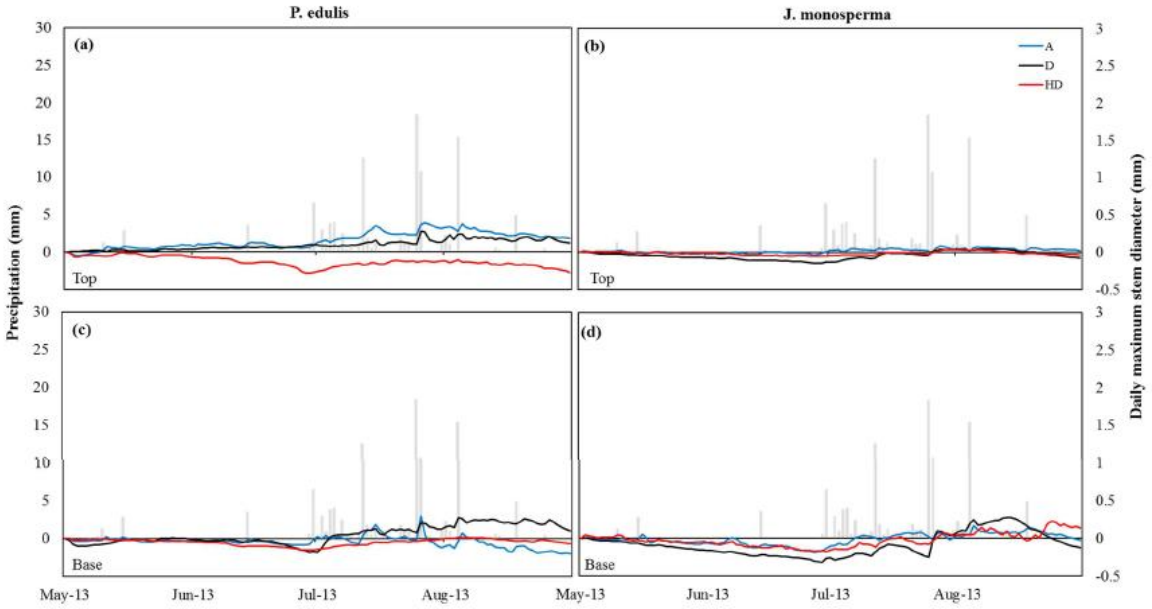

Figure 1. Time series of daily maximum stem diameter in base and top sensors of piñon pine and juniper during the growing period from May to September 2013 under 3 environmental treatments (ambient, drought, drought+heat). Piñon pine top sensors (a), juniper top sensors (b), piñon pine base sensors (c), juniper base sensors (d). Precipitation shown with vertical grey bars.

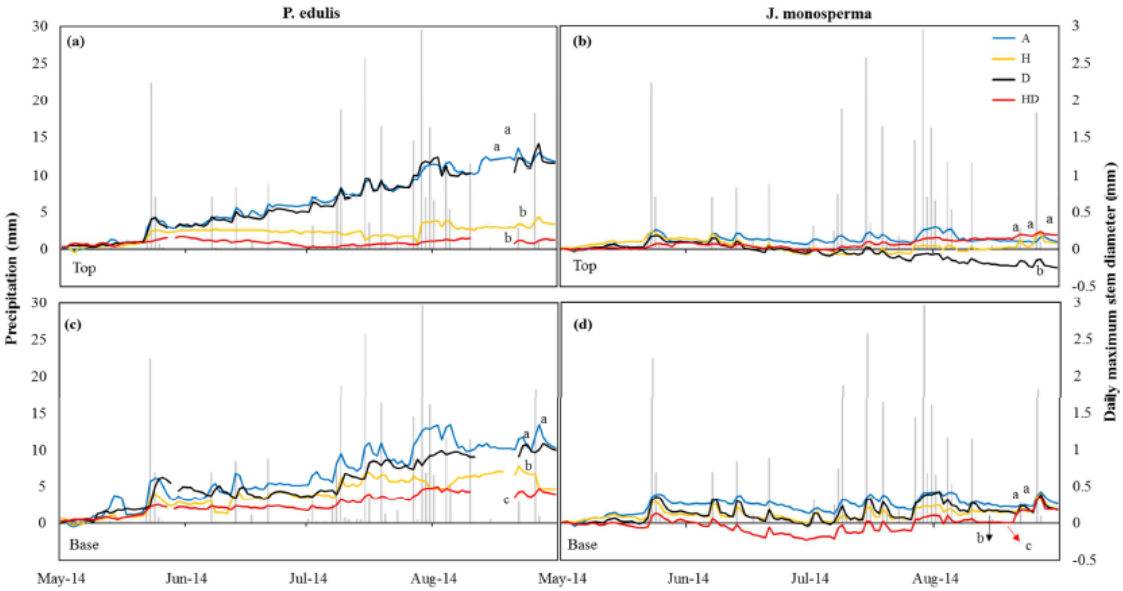

Figure 2. Time series of 2014 daily maximum stem diameter in base and top sensors of piñon pine and juniper during the growing period from May to September 2014 under 4 environmental treatments (ambient, drought, heat, drought+heat). Piñon pine top sensors (a), juniper top sensors (b), piñon pine base sensors (c), juniper base sensors (d). Letters indicate significant difference among treatments ($p < 0.0001$) over the season. Precipitation shown with vertical grey bars.

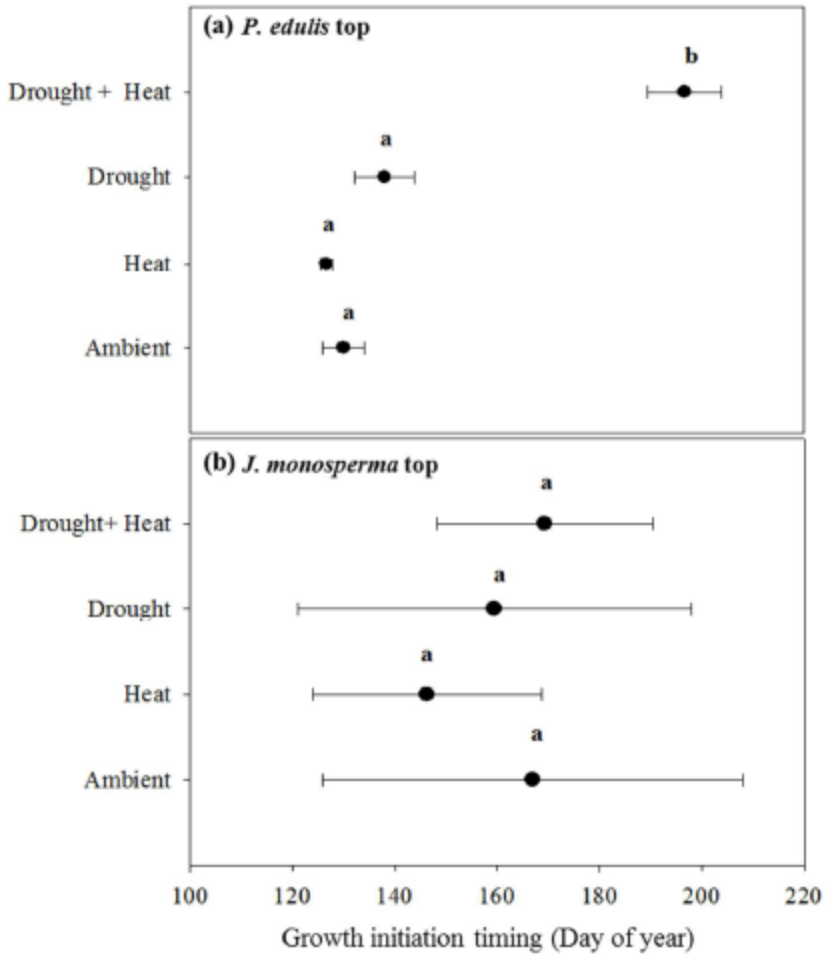

Figure 3. Mean timing of stem radial growth initiation for piñon top sensors (a) and juniper top sensors (b) during the 2014 growing season. Significant differences were found for growth initiation timing only in piñon top sensors, indicated with letters (ANCOVA $p < 0.05$). Error bars are standard errors.

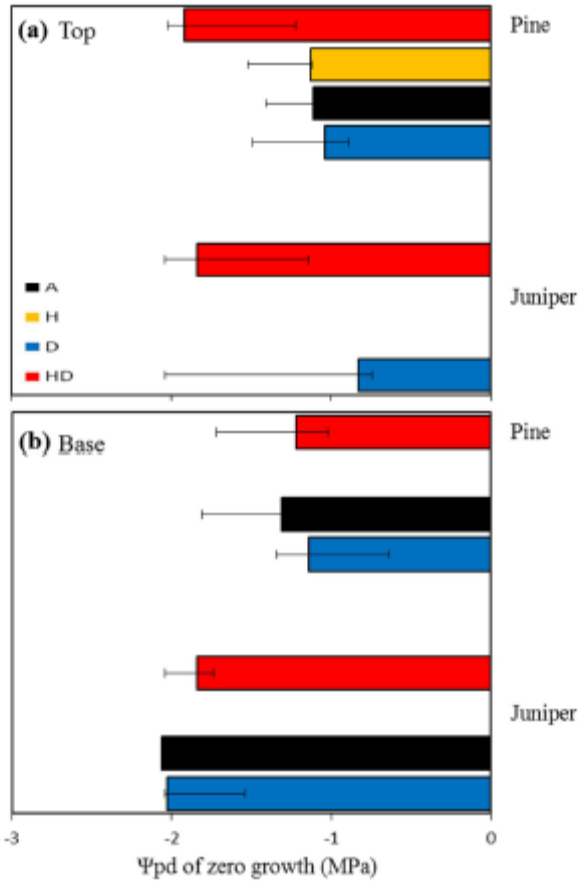

Figure 4. Mean predawn leaf water potential of zero growth for 2013 & 2014 by treatments (ambient, drought, heat, drought+heat). (a) top growth, (b) base growth. No treatment effect on Ψ_{pd} of zero growth was observed in either species. Error bars are the inflection point confidence interval (95%). Because inflection points could not be calculated from non-significant Weibull fit correlations (Fig S2, S3), mean Ψ_{pd} of zero growth is not shown for some species × treatment combinations.

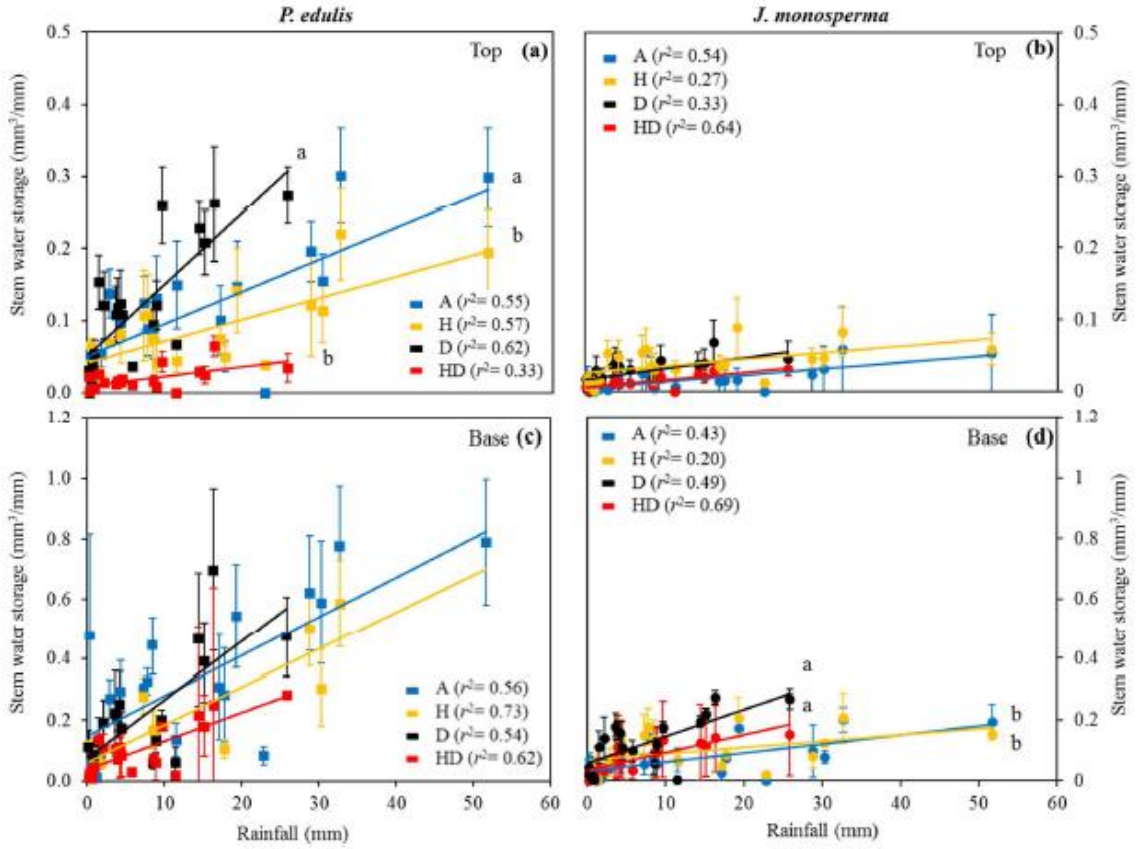

Figure 5. Relationships in piñon pine (square) and juniper (circle), between rainfall pulses and stem volume storage, calculated as the volume change at the location of the sensor and divided by the mean diameter of each tree to consider the differences in tree size; A=Ambient (blue), H=Heat (yellow), D=Drought (black), HD=Heat and drought (red). Piñon pine top sensors (a), juniper top sensors (b), piñon pine base sensors (c), juniper base sensors (d). Lines are shown for significant linear regressions ($p < 0.05$), and coefficients of determination are indicated in the legend for each panel. Significant differences among treatments are indicated with letters (ANCOVA, $p < 0.001$). Error bars are standard errors.